THE DEVELOPMENT OF BRYOZOAN FAUNAS IN THE UPPER PALAEOZOIC OF AUSTRALIA.

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(Four Text-figures.)

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Synopsis.

The development, sequence, and stratigraphic significance of bryozoan faunas in Australia during the Carboniferous and Permian are described in as much detail as is possible from the research so far carried out on this group. The distribution of bryozoan faunas during each period is first summarized; then the occurrence of any forms of stratigraphic significance in each area and the correlations which they suggest are considered; in conclusion, the evolution of the broad faunal provinces found in the late Palaeozoic of Australia, and the probable sources and relationships of the bryozoan faunas of these provinces are discussed.

LOWER CARBONIFEROUS BRYOZOAN FAUNAS.

Lower Carboniferous strata extend from the Hunter River in New South Wales to beyond Rockhampton in Queensland; small collections of Bryozoa from several localities within this area (Text-fig. 1) have yielded a comparatively large and varied fauna. The early Carboniferous saw the influx of new families and subfamilies of Bryozoa, and the disappearance of some of the older families or, where these families persisted, new genera of a distinctly Carboniferous type were evolved at this time; many of these new and specialized genera rapidly appeared in the faunas here (Tables 1 and 2). Correlation of Australian Lower Carboniferous horizons has been made by comparison of goniatite, coral, and brachiopod faunas with those of the Tournaisian and Viséan of Belgium or of England and Scotland; as few published descriptions of Bryozoa from western European faunas of this age are available, comparison of the bryozoan faunas is best made with those of the United States and Russia, and the Tournaisian-Viséan boundary of Europe is here regarded as approximating to the Osage-Meramac boundary of the United States, and the Viséan-Namurian boundary as lying at or near the top of the Chester Series (Cheyney et al., 1945).

THE AGE OF BRYOZOAN FAUNAS FROM THE BURINDI AND LOWER KUTTUNG SERIES.

The marine Burindi Series ranges from the base of the Tournaisian to the top of the Viséan, and is partly contemporaneous with the predominantly freshwater Lower Kuttung Series; the freshwater glacial beds of the Upper Kuttung are Upper Carboniferous (Text-fig. 2).

The main bryozoan horizon in the Burindi is that found at Glen William and Hilldale, and is some 200 to 400 feet below the top of the Lower Burindi Series at these localities. The occurrence of *Evactinopora*, *Fistulamina*, *Goniocladia*, and *Streblotrypa* all indicate an early Mississippian age for this fauna. *Evactinopora* first occurs in the Burlington and Keokuk Limestones in the United States; *E. trifoliata* is a distinctly more primitive form than any described from these Limestones and fixes the probable upward limit to the age of this fauna. *Fistulamina* (as *Meekopora* ? *aperta* Ulrich, 1890) also occurs in the Keokuk; typical species of *Streblotrypa* readily distinguished from the more primitive Devonian species appear in abundance in the early part of the Osage group; *Goniocladia* appears at the base of the Viséan in Russia and in the Lower Carboniferous of Scotland; and *Hemitrypa* is particularly abundant in the Keokuk, and *H. clarkei* closely resembles two Keokuk and Warsaw species. The fenestrate and pinnate Bryozoa from this horizon also bear a strong general resemblance to those described by McCoy in 1845 from the Lower Carboniferous limestone of Ireland, and several Burindi species, though now considered distinct, were originally identified by de Koninck (1878) with these Irish species. The occurrence of this group of genera in

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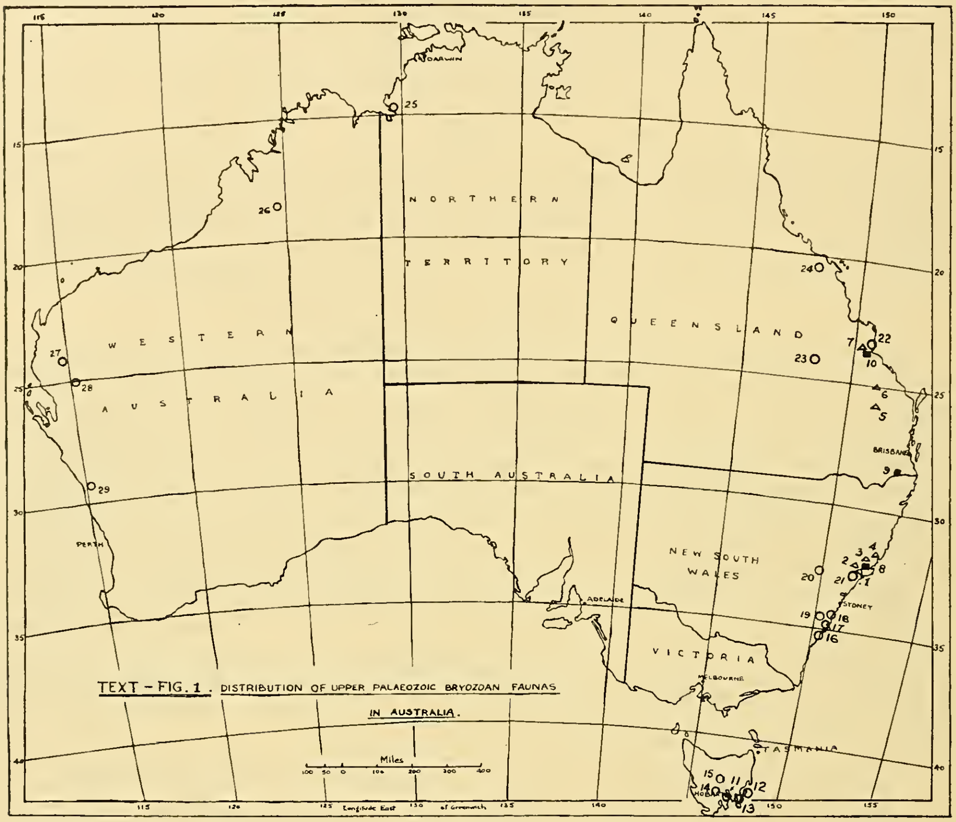
the top beds of the Lower Burindi Series, and the stage of development reached by species representing each of them, suggests an age equivalent to an early part of the Osage Series of the United States, and so to an horizon within the upper part of the Tournaisian.



Text-figure 1.—Distribution of Upper Palaeozoic Bryozoan Faunas in Australia. The principal localities to which reference is made in the text are indicated as follows:

Lower Carboniferous (△) : 1, Glen William and Hilldale; 2, Rouchel Brook; 3, Barrington; 4, Taree; 5, Mundubbera and Mundowran; 6, Cannindah; 7, Stanwell and Rockhampton.

Upper Carboniferous (■) : 8, Stroud; 9, Mt. Barney; 10, Stanwell and Rockhampton.

Permian (○) : 11, Hobart district; 12, Maria Island; 13, Eaglehawk Neck; 14, Fitzgerald; 15, Marlborough; 16, Ulladulla; 17, Gerringong; 18, Wollongong; 19, Bundanoon; 20, Rylstone; 21, Hunter River Coalfield; 22, Lake's Creek; 23, Springsure; 24, Bowen River Coalfield; 25, Port Keats; 26, Nooncanbah, West Kimberley; 27, Minilya River, North-West Basin; 28, Lyons and Gascoyne Rivers, North-West Basin; 29, Irwin River.

The fauna of the marine intercalation near the base of the Lower Kuttung at Rouchel Brook and Back Creek is not far separated (by coarse marine and volcanic sediments) from this Lower Burindi horizon; its fauna, though less varied, shows no distinctive differences from the Lower Burindi fauna and is assumed to be of closely similar age.

The bryozoan fauna occurring in the Burindi Series (undivided) at Barrington includes species of "*Batostomella*" and *Dichotrypa*. "*Batostomella*", congeneric with *B. spinulosa* Ulrich, 1890, is first recorded from the Ste. Genevieve Limestone of the Meramac Group in the United States, and in Russia this genus is listed (Nikiforova, 1933) from the Viséan, but is not known to occur in definitely Tournaisian localities. *Dichotrypa*, though one species occurs in the Middle Devonian, is particularly abundant in the St. Louis Limestone of the Meramac, and occurs also in the Viséan in Russia.

TABLE 1.

Distribution of Species in the Lower Carboniferous of N.S.W.

(The forms listed were described as new species by de Koninck, 1878, and Crockford, 1947.)

Species.	Lower Burindi.		Lower Kuttung.		Upper Burindi (?).	Upper Burindi.
	Glen William.	Hilldale.	Rouchel Brook.	Back Creek.	Barrington.	Taree.
Fistulipora mirari	×	×				
Dybowskiella rhomboidea						×
Evactinopora trifoliata	×					
Fistulamina inornata	×	×		×		
Goniocladia laxa		× (1)				
G. parva			×			
Ramipora (*Ramiporalia*) *bifurcata*	×					
"*Batostomella*" *lineata*					×	
*Fenestella** *propinqua*	×	×		×	×	
F. acarinata	×	×				
F. cribriformis			×			
F. roucheli			×			
F. barringtonensis					×	
F. cellulosa					×	
Hemitrypa clarkei	×	×				
Ptilopora konincki	×		×			
Dendricopora hardyi	(2)					
Penniretepora osbornei	×					
Streblotrypa parallela	×	×	×		×	
Dichotrypa fragilis					×	

(1) Original locality Burragood and Colo Colo.

(2) Original locality Burragood.

* The generic name *Fenestella* Lonsdale, 1839, is here used in preference to *Fenestrellina* d'Orbigny, 1849 : an application for suspension of the Rules of Zoological Nomenclature for the generic name *Fenestella* has been submitted to the International Commission on Zoological Nomenclature by G. E. Condra and M. K. Elias (*J. Paleont.*, 15, 1941, 565–6).

TABLE 2.

Distribution of Species in the Lower Carboniferous of Queensland.

(The forms listed were described as new species by Crockford, 1947.)

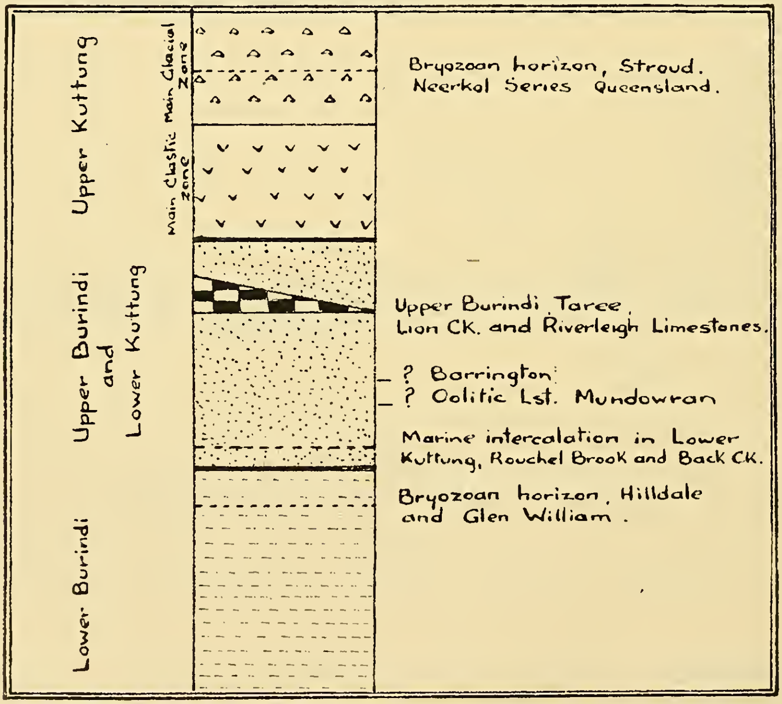
Species.	Oolitic Lst. Mundowran.	Lion Creek Lst.	Riverleigh Lst.	Cannindah Lst.
Fistulipora etheridgei		×		
Dybowskiella crescentica				×
Evactinopora irregularis	×			
Fistulamina malmoensis			×	
Ramipora (*Ramiporella*) *flexuosa*			×	
Leioclema porosa		×		
Stenodiscus stanwellensis		×		
Fenestella yarrolensis	×			
F., sp. indet.			×	
Polypora sulcifera			×	
Arcihmedes regina			×	
A. spiralis			×	
Penniretepora fragilis			×	
Rhabdomeson, sp. indet.	×			
Streblotrypa, sp. indet.				×

There is no direct field evidence of the stratigraphic position of this fauna; the presence of these two genera at Barrington, and their absence from the Hilldale–Glen William horizon, suggest that the Barrington fauna is slightly younger and should be correlated with part of the Meramac, rather than the Osage, Group of the United States, and is therefore of early Viséan age.

Dybowskiella, associated with *Fistulamina* and *Fistulipora*, occurs in the Upper Burindi Limestone at Taree; the coral fauna of this limestone is Upper Viséan in age.

THE AGE OF BRYOZOAN FAUNAS FROM THE LOWER CARBONIFEROUS OF QUEENSLAND.

Bryozoa have been described from the Lower Carboniferous at four localities in Queensland (Text-fig. 1; Table 2). The earliest of these faunas seems to be that of the oolitic limestone at Mundowran in the same district as the Riverleigh Limestone; the field and stratigraphic relationships of these limestones to each other are not known (Hill, 1934, 105). As well as *Evactinopora*, *Fenestella*, and *Rhabdomeson*, this oolitic limestone contains abundant fragments of specifically indeterminate Bryozoa, *Fistulamina*, *Fistulipora*, and batostomellids having been recorded from it. *Evactinopora irregularis* is more advanced than *E. trifoliata* of the Lower Burindi, and more closely approaches North American Burlington and Keokuk species; its zoarium was probably attached and its growth form is slightly irregular, so that it is probably no younger a species than the Burlington-Keokuk forms, in which the zoaria are free and their



Text-fig. 2.—The Carboniferous Sequence of the Northern Hunter Valley area of New South Wales, and the relative positions of the principal Bryozoan horizons.

growth form more stabilized. The presence of this form thus suggests that this horizon is of earlier age than the Riverleigh Limestone, and is equivalent to some part of the Osage Series and so to the topmost beds of the Tournaisian; but equivalent to a slightly higher horizon than the top part of the Lower Burindi, in which the more primitive *E. trifoliata* occurs.

The coral faunas of the Riverleigh and Lion Creek Limestones are Upper Viséan (Zone D2) in age or very slightly younger (Hill, 1943, 62). Two species of *Archimedes*

occur in the Riverleigh Limestone; though this genus first occurs in the earlier Keokuk-Warsaw beds in the United States, the greatest number of species occurs in the Chester Series, equivalent in age to the top of the Viséan; *Archimedes* first occurs in the western United States and Russia in the Lower Pennsylvanian. *Ramiporella flexuosa* is a more primitive form than the species of this subgenus described from the Upper Carboniferous of Russia. *Polypora* also first occurs in Australia in this limestone, and *Stenodiscus* appears in the Lion Creek Limestone, but each of these genera appears in an earlier part of the Lower Carboniferous in Europe and the United States.

Upper Carboniferous Bryozoan Faunas.

Bryozoa are abundant in the Neerkol Series at Stanwell, Rockhampton and Mt. Barney, and in a thin marine intercalation in the Upper Kuttung at Stroud (Table 3).

TABLE 3.

Distribution of Species in the Upper Carboniferous of Queensland and New South Wales.
(The forms listed were described as new species by Crockford, 1949.)

Species.	Neerkol Series.					Marine Intercalation in Upper Kuttung Series, Stroud.
	Ridge above Lion Creek.	Malchi Creek, Rockhampton.	Par. 2v, Par. Stanwell.	Mt. Barney, Pors. 193–4, Par. Palen.	Mt. Barney, Pors. 127v and 202, Par. Palen.	
Fistulamina frondescens ..						×
F. dispersa	×			×		
Leioclema ? sp.	×					
Fenestella malchi		×		×	×	×
F. osbornei	×	×	×	×		×
F. micropora	×					
F. barneyi			×	×		
F. cincta		×				
Polypora pustulosa			×			
P. neerkolensis			×	×	×	
P. palenensis					×	
P. tenuirama		×				
Penniretepora spp.		×	×			

Fenestellids have been recorded from the Kullatine Series in the Manning River district and the Emu Creek Series at Drake, but no specimens suitable for description have been collected. These Upper Carboniferous faunas (Crockford, 1949, 419) are characterized by the association of *Fistulamina* with abundant *Fenestella* and *Polypora*; they lack the variety found in Lower Carboniferous faunas, especially in the absence of fistuliporoids other than *Fistulamina*, and are distinguished from succeeding Permian faunas by the virtual absence of batostomellids and also the absence of *Protoretepora* and *Minilya*; while it is possible that faunas described so far have come only from zones in which fenestrate forms predominate and that other facies have been passed over in collecting, the collections have been made from many widely scattered localities and at present are regarded as representative.

Stratigraphic Use of the Bryozoan Faunas.

Generalized correlation between the Neerkol Series at the type locality near Rockhampton and at Mt. Barney and the Upper Kuttung is indicated by the bryozoan faunas (Crockford, 1949, 428). No species described from the Upper Carboniferous here is known to occur elsewhere, and all the genera present are known earlier as well as in the Upper Carboniferous; thus there is, unfortunately, no possibility at present of using these faunas for wider correlations. The Pennsylvanian of the United States and the Upper Carboniferous of Europe saw the introduction of many new forms with

TABLE 4.

Distribution of Species in the Permian of Eastern Australia.

Species.	New South Wales. Hunter Valley. Lower Marine. Allandale Stage.	New South Wales. Hunter Valley. Lower Marine. Rutherford Stage.	New South Wales. Hunter Valley. Upper Marine Series. Fenestella Shales.	New South Wales. Hunter Valley. Upper Marine Series. Muree Stage.	New South Wales. Hunter Valley. Upper Marine Series. Mulbring Stage.	New South Wales. South Coast. Upper Marine Series. Ulladulla Mudstones.	New South Wales. South Coast. Upper Marine Series. Wollongong & Gerringong.	Tasmania. Maria Island and Porter's Hill.	Tasmania. Marlborough.	Tasmania. Berriedale Lst.	Tasmania. Grange Quarry.	Tasmania. Eaglehawk Neck and Fitzgerald.	Queensland. Dilly Stage, Springsure.	Queensland. Lake's Creek Quarry.	Queensland. Middle Bowen Series.	Queensland. Gympie Beds.
Batostomella cylindrica Crockford						×										
Dyscritella porosa Crockford ..	×															
D. restis Crockford		×														
Stenopora johnstoni Etheridge ..	×	×						×								
S. etheridgei Crockford		×														
S. spiculata Crockford ..	×															
S. rugosa Crockford			×													
S. contigua Crockford ..				×												
S. crinita Lonsdale				×	×		×					×				
S. gracilis (Dana)							×									
S. nigris Crockford							×									
S. frondescens Crockford ..							×									
S. tasmaniensis Lonsdale ..										(1)						
S. ovata Lonsdale										(1)						
S. pustulosa Crockford										×						
S. hirsuta Crockford										×						
S. parallela Crockford										×						
S. grantonensis Crockford ..										×						
S. australis Nicholson and Etheridge															×	
S. jackii Nicholson and Etheridge															×	
S. leichardtii Nicholson and Etheridge															×	
S. gimpiensis Etheridge ..																×
Stenodiscus moniliformis Crockford										×						
Fenestella fossula Lonsdale ..	×	×	×			×			×	×	×		×			
F. dispersa (Crockford) ..	×	×	×			×			×	×	×		×			
F. exserta Laseron			×			×										
F. granulifera (Crockford) ..			×							×				×		
F. altacarinata (Crockford) ..			×			×										
F. quinquecella (Crockford) ..						×			×							
F. canthariformis (Crockford)			×										×	×		
F. horologia Bretnall													×			
F. aspratilis Bassler														×		
F. simulatrix (Crockford) ..														×		
F. sparsinodata (Crockford) ..														×		
F. rockhamptonensis (Crockford)														×		
F. sparsa (Crockford)														×		
F. spinifera (Crockford) ..														×		
F. expansa (Crockford) ..														×		
F. expansa var. *nodulifera* (Crockford)														×		
Hemitrypa sexangula Lonsdale..										(2)						
Minilya duplaris (Crockford)														×		
M. bituberculata (Crockford) ..			×													
Polypora pertinax Laseron ..	×	×														
P. virga Laseron	?		×			×			×							

TABLE 4.—*Continued.*

Distribution of Species in the Permian of Eastern Australia.—Continued.

Species.	New South Wales.							Tasmania.					Queensland.			
	Hunter Valley.						South Coast.									
	Lower Marine.		Upper Marine Series.													
	Allandale Stage.	Rutherford Stage.	Fenestella Shales.	Muree Stage.	Mulbring Stage.	Ulladulla Mudstones.	Wollongong & Gerringong.	Maria Island and Porter's Hill.	Marlborough.	Berriedale Lst.	Grange Quarry.	Eaglehawk Neck and Fitzgerald.	Dilly Stage, Springsure.	Lake's Creek Quarry.	Middle Bowen Series.	Gympie Beds.
P. woodsi (Etheridge) ..			×			×			×	×	×			×		
P. montuosa (Laseron) ..			×													
P. dichotoma Crockford ..						×										
P. triseriata Crockford						×										
P. multinodata Crockford ..			×													
P. magnafenestrata Crockford	×		×			×				×						
P. linea Crockford			×													
P. minuta Crockford														×		
P. smithii Etheridge																×
Protoretepora ampla (Lonsdale)				×						(2)						
P. konincki Etheridge															×	
Ptilopora carinata Crockford ..							(3)									
Rhombopora filiformis Crockford						×										
R. laxa (Etheridge)																×

(1) Mt. Wellington, Mt. Dromedary, and Norfolk Plains (Strzelecki).
(2) Originally described from an unknown horizon, Tasmania.
(3) Described from Crinoidal Stage, Shoalhaven Heads.

Permian affinities which existed under varied climatic conditions over a large part of the world; the absence of any of these new forms from the Upper Carboniferous here suggests that the eastern Australian geosyncline was already cut off by the beginning of the Upper Carboniferous from the free communication with other areas of Carboniferous sedimentation which was so evident in the Lower Carboniferous.

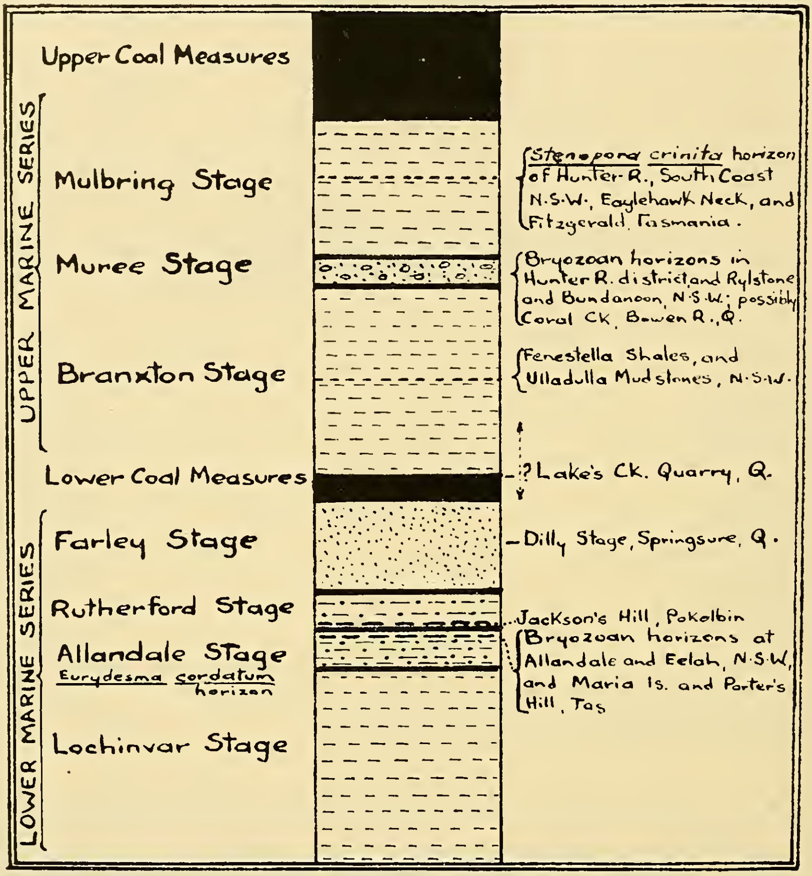
PERMIAN BRYOZOAN FAUNAS.

Permian marine sediments containing abundant bryozoan faunas are widespread in Australia; their occurrences fall into two distinct provinces in Eastern and Western Australia. Within these two broad provinces the faunas in the various basins of deposition show individual characteristics, but there are comparatively minor differences; some slight mingling of the two types of fauna occurs, mainly in northern Queensland.

THE EASTERN AUSTRALIAN PERMIAN FAUNAS.

Bryozoan faunas have been described from Hobart and Marlborough in Tasmania, the South Coast, Western, and Hunter River coalfields in New South Wales, and Rockhampton, Springsure, and the Bowen River in Queensland; faunas of the same general type occur in many other parts of these three States, but their faunas are less well known and are given only passing reference here. These Permian sediments extend for more than a thousand miles, but in spite of this and their great thickness and varied facies, the generic composition of the bryozoan faunas is remarkably uniform, and most genera present are long-ranged forms (Table 4); a small collection

of Bryozoa from the Permian of New Zealand in the Australian Museum collections belongs to the same general faunal type; no Bryozoa have been described from the Permian of New Zealand. The sequence in the Hunter River coalfield and the relative positions of bryozoan horizons in other districts are summarized in Text-figure 3.



Text-fig. 3.—Sequence in the Hunter River district, and the approximate relative positions of Bryozoan horizons in Eastern Australia.

Stratigraphic Use of the Bryozoan Faunas.

(a) Correlation within Eastern Australia.

Distinct bryozoan faunas from several horizons within two areas, the Hunter River-Western Coalfield-South Coast basin in New South Wales and the Hobart district in Tasmania, are recognizable and their faunas can to some extent be correlated.

In the Hunter River district the Lower Marine contains few Bryozoa below the base of the Allandale; specimens in the Lochinvar Stage, all fenestellids, are unfortunately specifically unrecognizable. The *Pecten* horizon at the top of the Allandale Stage contains abundant fenestellids, a few large stenoporids and fine ramose batostomellids; at the base of the overlying Rutherford Stage these fine batostomellids locally form bryozoal limestones. The stenoporids and other batostomellids of these horizons are distinct from those found in higher stages (Table 4); *Polypora pertinax* is also a common form in both horizons and several associated fenestellids as yet undescribed also appear to be of limited vertical range. *Stenopora johnstoni* and *Polypora pertinax* should be of value as index fossils for this section of the Lower Marine Series. The sandy sediments of the overlying Farley Stage are a facies unsuitable for Bryozoa;

their virtual absence is unfortunate, as important bryozoan horizons in other States occur in beds correlated with this stage.

Near the base of the Upper Marine, the Fenestella Shales contain an abundant bryozoan fauna; several species are restricted to this one band within the Branxton Stage (Table 4) and should be useful and easily identified zone fossils; on the South Coast this horizon and its characteristic fauna occur at Ulladulla, some two hundred miles distant. Stenoporids and other batostomellids are typically very rare throughout this stage. The Muree Stage contains many fenestellids, coarse species of *Polypora* being especially characteristic, but their preservation is usually too poor for description; *Protoretepora ampla* occurs in this horizon in the Western and Southern coalfields, and small zoaria of *Stenopora crinita*, in contrast to the very large zoaria developed later, first appear in the Muree. The Mulbring Stage is characterized by abundant large zoaria of *S. crinita* and of coarse ramose stenoporids, and by the extreme rarity of fenestellids and of the tiny ramose batostomellids found in earlier horizons; the large zoaria of *S. crinita* are distinctive and easily identified, and should be useful index fossils for this stage.

Bryozoan faunas from five localities in Tasmania can be closely correlated with these horizons. At Porter's Hill and Maria Is. the occurrence of *Stenopora johnstoni* indicates a horizon near the top of the Allandale, and at Maria Is. there is a *Eurydesma* zone just below the beds in which *S. johnstoni* occurs. The fenestellids at Marlborough suggest a horizon close to the Fenestella Shales. Large zoaria of *Stenopora crinita* occurring at Eaglehawk Neck and Fitzgerald show that these horizons are equivalent to the Mulbring Stage, and this agrees with the position of the beds at Eaglehawk Neck near the top of the marine Permian sequence there.

In the Hobart district the Permian is heavily faulted; faunas from Granton, Collinsvale, and Rathbone's Quarries (all in the Berriedale Limestone), and Glenorchy, Newtown, and Mt. Wellington have common features which suggest they are on the same

TABLE 5.

Distribution of Species in the Hobart District.

Species.	Berriedale Limestone.			Telosa Road, Glenorchy.	Newtown.	Huon Rd., Mt. Wellington, 1000 ft. above Sea Level.	"Mt. Wellington" of Strzelecki, Strickland Ave. Track, 1 m. W. of Cascade.
	Granton Quarry.	Collinsvale Quarry.	Rathbone's Quarry.				
Stenopora tasmaniensis ..							×
S. ovata							×
S. pustulosa		×	×	×	×	×	
S. hirsuta	×	×	×				
S. parallela						×	×
S. grantonensis	×						
Stenodiscus moniliformis ..		×					
Fenestella fossula						×	
F. dispersa						×	
F. granulifera						×	
Polypora magnafenestrata ..				×			

horizon (Table 5); the Berriedale Limestone has been considered to belong to the Lower Marine Series; of Bryozoa occurring both in this horizon and in New South Wales, only one is short ranged, and this form, *Fenestella granulifera*, though restricted to the Fenestella Shales in the Hunter district, occurs also at the top of the Dilly

Stage (correlated with the Farley Stage) in Queensland; its occurrence suggests a horizon either within the topmost beds of the Lower Marine or the basal beds of the Upper Marine Series. The rich fenestellid horizon of the Grange Quarry contains three species which occur in New South Wales; of these, *Polypora woodsi* is found only in the Fenestella Shales here, but is longer ranged in Queensland and Western Australia.

The Lake's Creek Quarry fauna in Queensland is Artinskian in age (Crockford, 1945, 125) but cannot at present be correlated with any one horizon in New South Wales. The top of the Dilly Stage at Springsure contains numerous stenoporids as well as the recorded fenestellids; this horizon has been correlated from other forms with the Farley Stage; the bryozoan fauna resembles that of the slightly younger Fenestella Shales, but the coarse sediments of the Farley Stage itself contain no recognizable Bryozoa. Species of *Protoretepora* and *Stenopora* were described by Nicholson and Etheridge from the Middle Bowen Series (Reid, 1930, 74; and Table 4); the stenoporids differ from those found elsewhere in eastern Australia in the small diameter of their tubes, only about half that generally found in eastern Australian species, irrespective of the size or shape of the zoarium itself; in this respect the Middle Bowen stenoporids strongly resemble those of the Permian of Western Australia. The presence of *Protoretepora* upon this horizon suggests correlation with the Muree Series and with the Nooncanbah Series in Western Australia.

(*b*) *Correlation with other Permian Faunas.*

The bryozoan faunas from the base of the Allandale Stage to the top of the Upper Marine Series are of Artinskian age, possibly ranging into the base of the Kungurian; there is no evidence from bryozoan faunas regarding the age of the Lochinvar Stage. The general type of fauna which appeared well developed in the Allandale and in rocks of equivalent age in Tasmania persisted without great change through almost all of the Permian sequence; the stenoporids in particular of the Allandale Stage are of a well-marked Permian type. *Polypora woodsi* indicates a Lower Permian age for the Branxton Stage and equivalent horizons; *P. woodsi* is the Artinskian representative of the *P. elliptica* gens (Elias, 1937, 327), which shows well-marked progressive variation from the base of the Carboniferous into the Permian. The occurrence of *Minilya* in the Branxton Stage and of *M. duplaris* at Lake's Creek also indicates a Lower Permian age; *Minilya* first appears at the top of the Pennsylvanian, and *M. duplaris* is a widespread Artinskian species. *Fenestella horologia*, which occurs in the Dilly Stage, is also an Artinskian form. The occurrence of *Protoretepora ampla* in the Muree and in the Nooncanbah Series of Western Australia supports correlations of these horizons; the Nooncanbah Series probably lies at the top of the Lower Permian, and the Muree is also probably upon or very near this horizon. Thus the Mulbring Stage and the Eaglehawk Neck beds may be basal Kungurian; it is notable that in these beds fenestellids are virtually absent and giant batostomellids such as *Stenopora crinita* have become abundant; fenestellids rapidly disappear at about the top of the Artinskian throughout the world and the stenoporids also disappear early in the Kungurian, the development of giant forms being a typical final development of an evolutionary line before extinction.

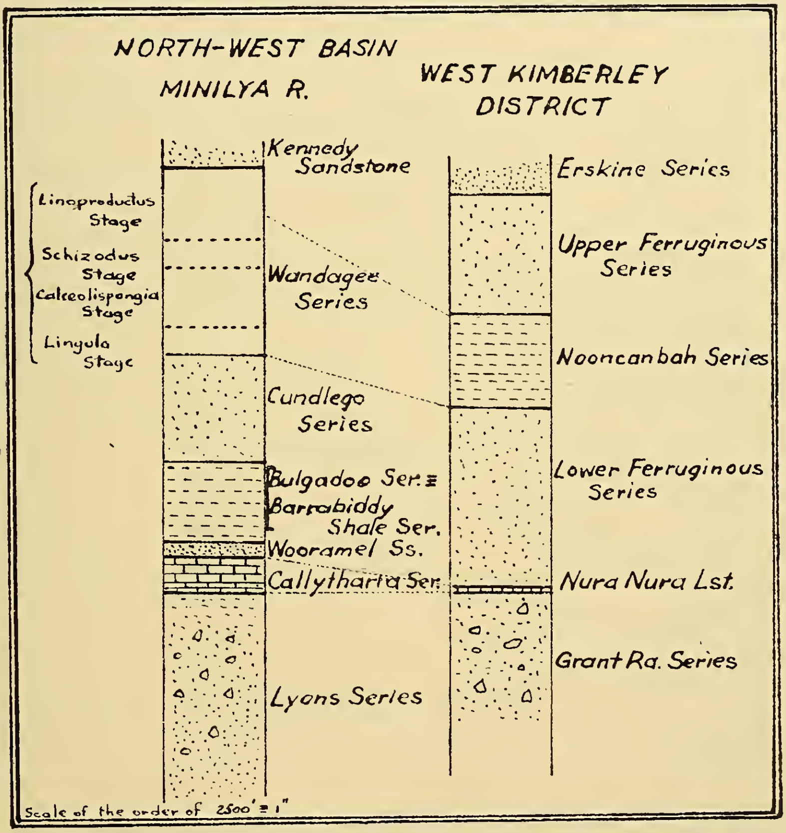
Many attempts have been made to correlate eastern Australian and Indian late Palaeozoic sequences; in these attempts the occurrence of several Bryozoa has been widely quoted, particularly the occurrence of forms described from Tasmania by Lonsdale (1844, 1845). These identifications have been discussed in detail in the revisions of each species described by Lonsdale; while none of the figured specimens from India seem to be conspecific with the eastern Australian types, there is a marked general similarity in the groups of genera present in the Anthracolithic Series of Kashmir particularly and the eastern Australian Permian, and the stage of development reached by several genera common in both areas, and especially of the stenoporids, *Fenestella* and *Protoretepora*, suggests a generally similar time range for the sediments in which they occur; but beyond this the bryozoan faunas do not at present give any evidence for precise correlation between the various stages of the eastern Australian

sequence and the Indian late Palaeozoic; closer comparison is at present possible between the more varied faunas of the Western Australian province and the Salt Range faunas of India.

The Western Australian Permian Faunas.

Bryozoa are abundant in the Permian sediments of the Irwin River, North-West Basin, and West Kimberley districts; the generalized sequence in each of these areas is shown in Text-figure 4; the stratigraphy has been summarized by Teichert (1946). Marine strata containing similar Bryozoa were cut in bores at Port Keats, on the west coast of the Northern Territory; this fauna also is discussed here. These areas of Permian deposition extend for some 1,000 miles from Port Keats south-west to the Irwin River.

The Bryozoa so far described from the Western Australian Permian are listed and their stratigraphic distribution summarized in Table 6; a number of specialized Permian genera, as well as long-ranged forms, occur, and though only a small proportion of the species present are known elsewhere (Table 7), many of those described from Western



Text-fig. 4.—Generalized section of the Permian sequence in Western Australia (after Teichert, 1941, 390).

Australia show clear affinity with Permian forms from other areas; the relationships of individual species have been discussed previously in descriptive papers. The fauna of the Fossil Cliff horizon in the Irwin River district is not listed separately, since descriptions of the main collections from this horizon, sent to the United States for study by Moore and Bassler, are not yet published and only small collections at present remain in Australia; in these the fauna appears generally similar to that found in the Callytharra. Another group in the Western Australian faunas which has as yet

TABLE 6.

Distribution of Species in the Permian of Western Australia and the Northern Territory.

Species.	Callytharra.	Barrabiddy Shale Series.	Cundlego.	Calceolispongia Stage, Wandagee.	Linoproductus Stage, Wandagee.	Nooncanbah.	Port Keats.
Fistulipora vacuolata Crockford						×	
F. wadei Crockford						×	
F. compacta Crockford				×			
F. conica Crockford				×			
F. gigantea					×		
Dybowskiella geei Etheridge							×
D. crescens (Crockford)						×	
Hexagonella australe (Bretnall)	×						
H. dendroidea (Hudleston)	×						
H. densa Crockford		×					
H. nalbia Crockford					×		
H. undulata Crockford					×		
H. bifida Crockford						×	
H. lineata Crockford						×	
H. plana Crockford						×	
Evactinopora crucialis Hudleston	×						
Goinocladia timorensis Bassler						×	
Ramipora ambrosoides (Bretnall)	×			×	×	×	
"*Sulcoretepora*" *meridianus* (Etheridge)						×	
Stenopora sp. "A" Etheridge						×	
S. sp. "B" Etheridge		×					
S. sp. "C" Etheridge						×	
Fenestella horologia Bretnall	×			×	×	×	×
F. affluensa Bretnall	×						
F. chapmani (Crockford)	×						
F. sparsigemmata (Crockford)	×						
F. alia (Crockford)	×						
F. disjecta (Crockford)					×	×	
F. columnaris (Crockford)	×						
F. ruidacarinata (Crockford)						×	
F. valentis (Crockford)						×	
F. lennardi (Crockford)						×	
F. cacuminatis (Crockford)						×	
Minilya duplaris (Crockford)				×		×	
M. princeps (Crockford)						×	
M. amplia (Crockford)	×						
Protoretepora ampla (Lonsdale)						×	
P. australis (Hinde)	×						
Lyropora erkosoides Etheridge	×						
Polypora forea Crockford				×			
P. retificis Crockford				×			
P. woodsi (Etheridge)	×					×	
P. multiporifera Crockford				×		×	
Penniretepora triporosa Crockford	×						
P. granulata Crockford	×						
P. fossata Crockford	×						
Septopora ornata Crockford	×						
Synocladia spinosa Crockford			×				
Rhabdomeson mammilata (Bretnall)						×	
Rhombopora tenuis (Hinde)	×						
R. hindei Etheridge							×
Streblotrypa browni Etheridge							×
S. marmionensis Etheridge	×	×	×	×	×	×	
S. etheridgei Crockford						×	
Rhombocladia minor Crockford	×						
R. spinulifera Crockford						×	
Streblocladia excavata Crockford	×						

received little attention is the Batostomellidae, which are abundantly represented by *Stenopora*, *Batostomella*, and closely related forms; the wide distribution of batostomellids in collections from most areas in Western Australia has been shown by the numerous records of their occurrence in faunal lists in stratigraphic papers, but so far this group has received little attention in descriptive work.

Stratigraphic Use of the Bryozoan Faunas.

(*a*) *Correlation within Western Australia.*

The occurrence in the Western Australian sequence of *Penniretepora*, *Lyropora*, *Septopora* and *Streblocladia* is restricted to the Callytharra Series; not a single specimen of any of these genera has been found in large collections from other horizons. The Callytharra is also characterized by the presence of numerous ribbon-like zoaria of *Hexagonella*, and by a group of fenestellids which, though some are long-ranged, contains a large proportion of species quite distinct from those found on higher horizons. The apparent absence of *Goniocladia*, *Stenopora*, and *Synocladia*, and the comparative rarity of *Fistulipora*, in the Callytharra is also notable.

Synocladia is common in and characteristic of the Cundlego Series and is not known on any other horizon in Western Australia.

Table 7.

Distribution of Species Common to the Permian of Western Australia and Localities Elsewhere.

Species.	Distribution in W.A.	Occurrences Elsewhere.
Goniocladia timorensis ..	Nooncanbah.	Basleo Beds, Timor.
Ramipora ambrosoides ..	Callytharra to Wandagee and Nooncanbah.	Basleo Beds, Timor (as *Acanthocladia acuticostata* Bassler.
Fenestella horologia	,, ,, ,,	Bitaoeni to Basleo Beds, Timor, and Permian, Vancouver Is. (as *F. parviuscula* (Bassler)); Dilly Stage, Qld.
Minilya duplaris	,, ,, ,,	? Middle Productus Lst., Salt Ra. (as *F. perelegans* Meek); Dilly Stage, and Lake's Ck., Qld.
Polypora woodsi	Callytharra and Nooncanbah.	Bitaoeni Beds, Timor (as *P. tripliseriata* Bassler); Dilly Stage and Lakes Ck., Q'ld.; Upper Marine, N.S.W.; Granton, Tas.
Protoretepora ampla ..	Nooncanbah.	Muree Stage, N.S.W.
Rhabdomeson mammillata ..	,,	Anthracolithic Series, Southern Shan States (as *R. shanse* Reed).
Streblotrypa marmionensis	Callytharra to Wandagee and Nooncanbah.	? Basleo and Amarassi Beds, Timor (? = *S. germana* Bassler).

The Wandagee and Nooncanbah Series are characterized by abundant massive and coarse ramose *Fistulipora*; by broad frond-like species of *Hexagonella* which, although they do occur on other horizons, are particularly characteristic of the higher beds of the Permian sequence; by the common occurrence of *Goniocladia* and the presence of *Protoretepora*; and by the distinct species of other genera such as *Fenestella*, *Polypora*, *Minilya*, *Rhombopora* and *Rhabdomeson*, in all of which, though they include some long-ranged forms, there are several species which are restricted to these higher beds. Massive and coarse ramose stenoporids are also very common in both series. These faunas of the Wandagee Series of the North-West Basin and the Nooncanbah Series of the West Kimberley district bear a strong general resemblance to each other, and as more research is done the number of species common to both will be greatly increased. The fact that, excluding long-ranged forms, only three species have been recorded as common to both series does not give a true picture of their relationship, and reference to published descriptions will show the similarity between several other species from these two areas. Four stages within the Wandagee Series have been differentiated by

Teichert (1946, 99); several described fenestellids and fistuliporoids are restricted to a single stage within this series (Crockford, 1944, Table 1; 1946, 145–154).

The fauna described from Port Keats contains only two long-ranged species in common with other localities in this province; no precise correlation of the Port Keats horizon is possible at present, but in its general aspect this small fauna resembles the Callytharra fauna much more closely than those of higher series.

(*b*) *Correlation with Eastern Australia.*

The occurrences of several species common to both provinces (Table 7) and the close similarity already noted between stenoporids from the Middle Bowen and Western Australian species indicate that the faunas of these two provinces, despite the fundamental differences in their aspect, are of similar time range within the Permian. Only one species appears to be of definite value in closer correlation: *Protoretepora ampla*, the occurrence of which supports correlation of the Nooncanbah with the Muree Stage of the Upper Marine Series.

(*c*) *Correlation with other Permian Faunas.*

Only seven species occurring in the Western Australian Permian are known from localities outside Australia (Table 7), but the stage of development reached by many of the genera present in the fauna and the occurrence of several rare and specialized forms give information of stratigraphic value. The Western Australian faunas show most affinity with those described by Bassler (1929) from Timor and with the Middle and Upper Productus Limestone faunas of the Salt Range; in addition, several Callytharra species, and the fistuliporoids throughout the sequence, are similar to late Pennsylvanian and Permian forms from midcontinental North America.

The Callytharra fauna shows a strong general resemblance to the fauna of the Graham Formation of the Cisco Group at the top of the Pennsylvanian of Texas described by Moore (1929), and of the Upper Pennsylvanian of Oklahoma described by Warthin (1930); Raggatt and Fletcher (1936) have previously suggested correlation between these horizons; they were probably deposited in very similar facies and at not widely differing times, but no species are now considered common to these two areas. On the other hand, the Callytharra contains at least five species (Table 6) in common with the higher beds of the Western Australian sequence, and each of these five species occurs in Artinskian but not in older strata elsewhere (Table 7). In addition, *Hexagonella australe* and other ribbon-like species of this genus common in the Callytharra represent a similar stage of development to *H. turgida* Bassler, 1929, from the Basleo and Amarassi Beds of Timor, and to the genotype from the Middle and Upper Productus Limestones of India, and *Hexagonella* is not known from pre-Artinskian strata in any part of the world; *Septopora ornata* is more closely related to species described from the Somohole and Bitaoeni Beds of Timor than to Russian and North American late Carboniferous species; *Streblotrypa marmionensis*, which first appears in the Callytharra, possesses the central bundle of small tubes characteristic of Permian species of this genus, and is probably identical with a species described from the Basleo and Amarassi Beds of Timor; and *Polypora woodsi* is a widespread Artinskian species and is the Lower Permian representative of the *P. elliptica* genus of Elias (1937, 327). *Evactinopora* and *Lyropora*, both of which have not elsewhere been recorded from post-Mississippian horizons, occur in the Callytharra, and *Evactinopora* also in higher beds of the Permian sequence; while the described species of *Lyropora* is a typical form of this genus, *Evactinopora crucialis* (Hudleston, 1883, 593; Etheridge, 1903, 9) is more advanced in zoarial form than any Mississippian species, and the presence of these two genera does not suggest any correlation of the Callytharra with Carboniferous horizons. The bryozoan faunas indicate that the Callytharra should be correlated with the early part of the Artinskian, and probably, therefore, with the Bitaoeni Beds of Timor (cf. Teichert, 1941, 399). Teichert also correlates the Callytharra with the Lower Productus Limestone of the Salt Range; Bryozoa are apparently uncommon in the Lower Productus Limestone; the Callytharra faunas show some resemblance to those of the Middle and Upper Productus Limestones, but this

resemblance is not so strong as that between the Wandagee and Nooncanbah faunas and those of the Middle and Upper Productus Limestones.

Synocladia is restricted to the Cundlego Series; similar species of this genus also appear in abundance in the Middle Productus Limestone and continue into the Upper Productus Limestone, and other similar species have been described from the Permian of England and Germany. The Cundlego fauna is of definite Artinskian age and should probably be correlated with an early part of the Middle Productus Limestone.

The Wandagee and Nooncanbah faunas show their closest resemblance to those of the Timor Permian; the resemblance is rather more marked in comparing the Wandagee and Nooncanbah with the higher stages, the Basleo and Amarassi Beds, than with the Bitaoeni Beds. This is particularly noticeable in comparing the abundance of massive and coarse ramose species of *Fistulipora* in the Wandagee and Nooncanbah with the sudden abundance of similar forms with comparable internal structure in the Basleo and Amarassi Beds, and it is also noticeable that *Sphragiopora*, which occurs only in the Amarassi, and *Goniocladia*, which occurs only in the Basleo Beds, are both quite abundant in the higher beds in Western Australia, but do not occur in the earlier stages. Five species are known to be common to these higher beds in Western Australia and the Timor Permian sequence (Table 7); but only one, *Goniocladia timorensis*, is of restricted range in both areas, occurring only in the Nooncanbah and in the Basleo Beds. Species of *Hexagonella* occurring in the Wandagee and Nooncanbah Series, and also *Streblotrypa etheridgei* from the Nooncanbah, are distinctly more advanced species than any described so far from Timor, and this is true also of coarse specimens of *Goniocladia* which occur frequently in collections from the Wandagee and Nooncanbah. The Bryozoa, therefore, suggest correlation of these two series with a slightly higher horizon than that indicated by Teichert (1941, 399), and to be possibly slightly younger, and at least no older, than the Basleo Beds.

Teichert (*loc. cit.*) also correlates the Wandagee and Nooncanbah with the top part of the Lower Productus Limestone of India. The bryozoan faunas suggest that the Western Australian sequence from at least the Cundlego Series upwards is younger than the Lower Productus Limestone; the general aspect of the bryozoan fauna which appeared in the Middle and persisted into the Upper Productus Limestone is closely similar to that of the Wandagee and Nooncanbah. The similar stage of development of internal structure in species of *Fistulipora* and *Dybowskiella* present in both areas, and the affinity of species of *Goniocladia* is again noticeable, while the zoarial form in species of *Hexagonella* from these higher beds in Western Australia seems to be of later development than that of any described Salt Range species; and among the fenestellids, though so far only one species is probably common to both areas (Table 7), there is distinct similarity between other species, especially in the occurrence in both areas of *Protoretepora* s. str. It does not appear possible that the Wandagee and Nooncanbah Series could represent a horizon earlier than one within the Middle Productus Limestone. The bryozoan faunas of these two series therefore suggest either a late Artinskian or an early Kungurian age for the horizons on which they occur.

The Development of Faunal Provinces during the Upper Palaeozoic.

The bryozoan fauna of the Lower Carboniferous in eastern Australia migrated freely and rapidly between this and other areas of early Carboniferous deposition. This migration was from the north, the fauna being of the same general type as that found contemporaneously in central North America and Europe. The mild, cold, temperate climate during the Tournaisian favoured the development of the varied fauna found; the seas commenced to withdraw to the north during the early Viséan and the climate became sub-glacial, but rapid migration of faunas from this same Tethyan source remained possible until the close of the Viséan, and this fauna quickly re-established itself in the brief warmer intervals represented by the Upper Viséan reef limestones.

The Upper Carboniferous was a period of intense glaciation in New South Wales, where the freshwater facies of the Hunter River passes northwards into predominantly

marine sediments in northern New South Wales and Queensland. The bryozoan faunas appear to be the remnant, restricted by adverse climatic conditions, of the earlier Carboniferous faunas; they appear, from the persistence of *Fistulamina* and the virtual absence of batostomellids, to be more closely related to these earlier faunas than to those of the succeeding Permian. By the Upper Carboniferous eastern Australia was probably cut off from free migration of faunas from the north, for there is no evidence of any one of the numerous genera of Bryozoa which were at that time evolving in the North American and European seas.

In the Lower Permian an abundant Tethyan fauna resembling that of the Lower Carboniferous of eastern States re-appeared in Western Australia. These faunas were clearly derived from a common faunal source, the early Carboniferous derivatives which migrated along the east coast being primitive representatives of genera which much later, having reached a higher stage of their development, migrated into the Permian basins of Western Australia. This widespread late Palaeozoic fauna did not migrate as far as eastern Australia during the Permian.

The wide divergence between the eastern and Western Australian faunas is not due to any difference in age, since the bryozoan faunas of Western Australia are the Permian representatives of a general type of fauna which existed for a long part of the Upper Palaeozoic, and the generally similar time range of the different areas of Permian sedimentation in eastern and Western Australia has long been established; nor is difference in facies sufficient reason for the distinct faunas, since Bryozoa are abundant in many different types of facies in both areas.

The Western and eastern Australian faunas have frequently been referred to as "warm-" and "cold-water" faunas respectively, and difference in climate in part accounts for the distinct faunas, but seems insufficient to do so fully. The type of fauna and the groups of genera found in the Western Australian Permian are spread over so large a part of the world that they must have been able to exist under a considerable variety of climatic conditions; intermittently the climate of eastern Australia, especially of New South Wales and Tasmania, was extremely cold during the Permian, and in some cases glacial erratics are associated with abundant Bryozoa; but some of the interglacial epochs were of long duration and the climate must then have been milder, and earlier, during the Lower Carboniferous, a varied bryozoan fauna rapidly reappeared during such milder intervals. In Western Australia also intermittent glaciation occurred during the Permian, and one glacial horizon, the Nura Nura Limestone of the Kimberley district, is correlated with the Callytharra Series of the North West Basin, which contains an abundant and varied bryozoan fauna, especially fistuliporoids. The great distance through which Permian deposits are distributed in eastern Australia must, like the interglacial epochs, have afforded some appreciable difference in climate, but the generic assemblage of Bryozoa is unvaried.

Limited migration between these provinces was possible during at least a part of Permian time, as shown by the occurrence of a few identical species in Queensland, Western Australia, and Timor, and to a lesser extent in comparing the faunas of New South Wales and Tasmania with those of Western Australia (Tables 4, 7); the occurrence of generally similar types of stenoporids in the Bowen River coalfield and in Western Australia also suggests relationship between the faunas of these two areas. This slight intermingling of faunas occurs earlier in Queensland, in the Dilly Stage, than in New South Wales, where the first evidences of migration are seen in the early part of the Upper Marine Series; but the fauna of each province retained without appreciable modification its own characteristics until marine Permian sedimentation ceased.

The eastern Australian Permian faunas may have been developed during the early part of the Permian from the poor and restricted Neerkol faunas, or were more probably (because of the absence of *Fistulamina* or any form derived from it, and because of the abundance of batostomellids, which were virtually absent from the Neerkol) faunas which migrated from a southern source northwards along the east coast of Australia.

The strong resemblance between the Tasmanian faunas and those of the Hunter Valley–South Coast Basin in New South Wales, and the gradual lessening of these resemblances through the central north coast basin in New South Wales and the areas of Permian deposition in Queensland also suggest that the eastern Australian faunas as a whole migrated from the south northwards; such migration was possibly influenced by cold south to north currents developed around the coastline of that time, and such currents could have been an effective barrier to any large-scale migration of the Tethyan faunas into the eastern Australian province.

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